

FURTHER MORPHOLOGICAL STUDIES ON ANASTOMOSES IN THE DICHOTOMOUS VENATION OF CIRCAEASTER

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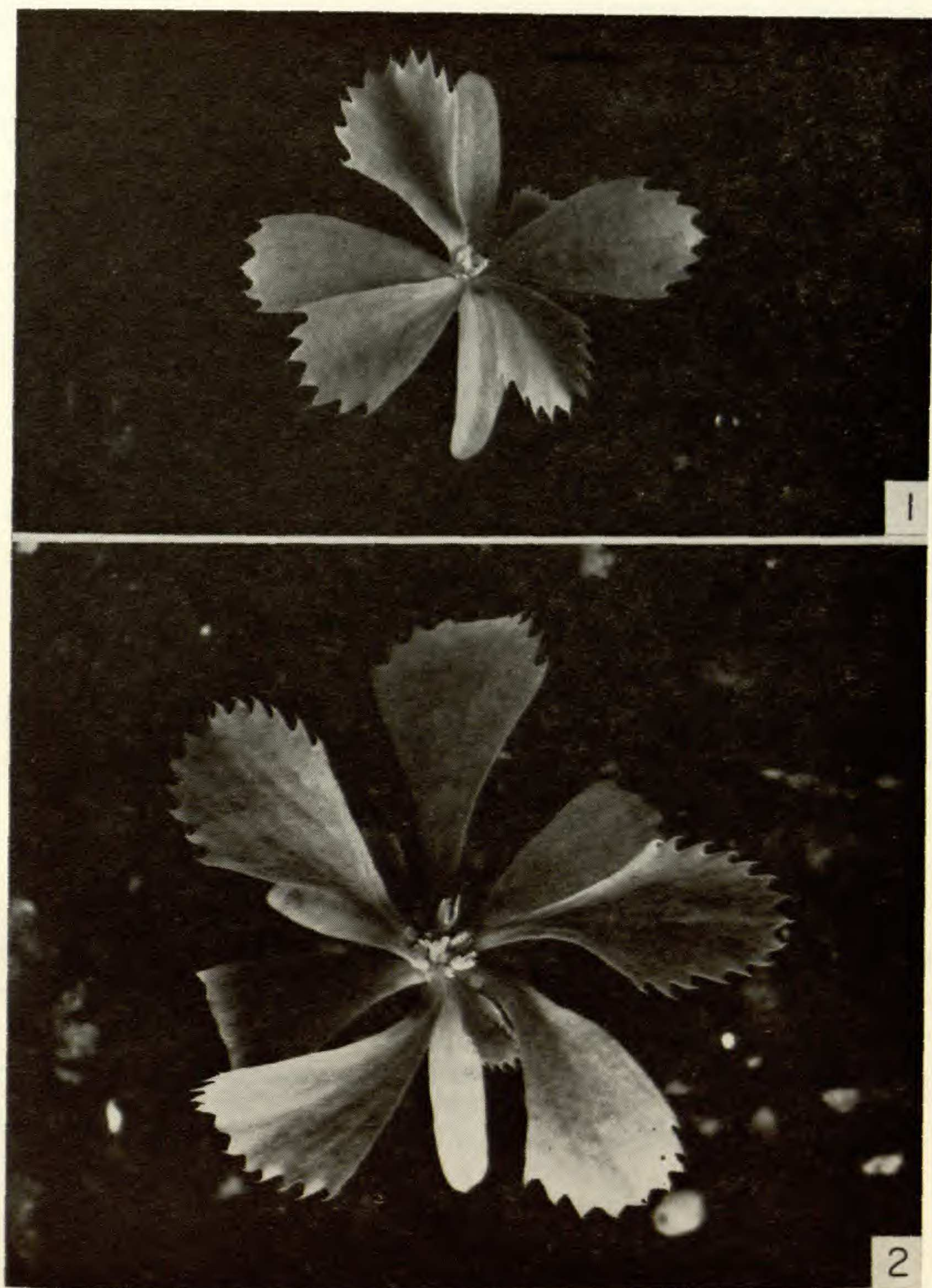
CONTINUED RESEARCH ON DICHOTOMOUS LEAF VENATION in specimens of *Circaeaster agrestis* Maxim. grown at the University of California Botanical Garden, Berkeley, during 1965 and 1966 revealed that the three kinds of anastomoses described in my last paper (Foster 1966) do not include the full range of variation in types of vein unions which are developed in this genus. The main purpose of the present article, therefore, is to describe the additional forms of anastomoses and their associated vein approximations which have been found, and to compare their morphology with the types previously considered.

A further objective of this paper is to present a brief account of the early phases of development of the seedling and the complex organography of mature flowering and fruiting specimens. This phase of my study is illustrated by photographs of living plants (FIGS. 1-3) which it is believed will convey a realistic idea of the general organization and development of the leaf-rosette and the condensed fascicles of flowers characteristic of this remarkable little dicotyledonous herb.

MATERIALS AND METHODS

The cultivated plants which provided the material for this study were grown during 1965 and 1966 from the collection of fruits given to me through the kindness of Dr. M. Anantaswamy Rau, Regional Botanist of the Botanical Survey of India. He had collected these fruits on October 22, 1963, from the colonies of *Circaeaster* originally discovered in 1962 by Bhattacharyya (1964) "growing gregariously on shady and flat mossy rocks under the shade of *Viburnum* bushes" near Gangharea, North Garhwal, India, "at an altitude of nearly 3300 meters."

Fruits were stored at a temperature of approximately 40°F until needed and under such conditions retained for more than three years an ability to germinate. The seedlings were raised in pots of soil in a growth chamber illuminated for 16 hours a day and maintained at a constant temperature of 42° F. Some variation in the time required for germination was noted over the successive years but in general a period of 3 to 4 weeks elapses before the conspicuously elongated hypocotyl elevates the cotyledons above the surface of the ground. Young plants were kept in the growth chamber for about a month during which time a series of leaves and, in some plants, the first fascicles of flowers were formed. The plants were then taken to the Botanical Garden, transplanted into small individual pots and placed



FIGS. 1 and 2. General organography of young cultivated specimens of *Circaea* photographed from above to show the cotyledons and primary leaves. 1, seedling, with two linear cotyledons and six expanded primary leaves. 2, older stage. The small structures in the center of the rosette are young involute leaves. Both figs. $\times 3$.

either in a lath house or a cool greenhouse. Mature fruits collected from potted plants during mid- or late summer of 1966 have proved viable and some of them this spring (1967) are producing a new crop of seedlings in

the growth chamber. Seedlings are also now developing in the open from fruits which had fallen from a group of plants which were grown last year in an especially prepared bed in the rhododendron dell in the Botanical Garden. It is hoped that from these plants a "permanent" colony may become established, comparable to the colonies maintained for a number of years at the Botanical Gardens at Upsala and Edinburgh (Foster 1963, p. 302).

When fully mature, the leaf-rosettes of a large number of plants were either preserved directly in 70 percent alcohol or in some cases were first killed and fixed in formalin-acetic acid-alcohol before storage in alcohol. All of the foliar organs of each plant (including the innermost small bracts of the flower-fascicles) were subsequently removed by means of small scissors, carefully examined for vein approximations and anastomoses, and the data recorded in tabular form. The leaves selected for venation studies were cleared in 5 percent NaOH followed by concentrated chloral hydrate, dehydrated in the usual alcohol series, stained in a 1 percent solution of safranin in equal parts of absolute alcohol-xylene and mounted in "Piccolyte."

I am extremely grateful to Mrs. Irene Baker, who has undertaken each year the planting of the fruits and has kept careful records of the beginning and the extent of the period of germination and early development of the seedlings. The line drawings in this paper represent direct tracings of photomicrographs and were prepared by Mrs. Emily R. Reid. I wish also to thank my wife for her assistance in proof-reading the manuscript.

ORGANOGRAPHY OF SEEDLING AND ADULT PLANT

The present description of the germination and general organographic development of *Circaeaster* is intended to supplement my previous account which was based entirely upon the study of a very limited number of herbarium specimens (Foster 1963, pp. 304-306).

During the early phases of germination, the curved, elongating hypocotyl, bearing the pair of closely appressed cotyledons at its apex, emerges from the soil. As a result of differential elongation, the hypocotyl soon becomes erect and the two linear cotyledons reflex and assume a horizontal position. These appendages remain green and persist throughout the life of an individual plant.

Approximately a week after the cotyledons have reflexed, a series of small, cuneate primary leaves begins to expand (FIGS. 1 and 2). The form and relatively simple dichotomous venation patterns of these earliest foliage leaves has already been described (Foster 1963, pp. 308, 309). The venation of the primary leaves, like that of the adult type of leaf, is involute.

As elongation of the hypocotyl continues, the terminal rosette becomes large and morphologically complex because of the development of additional crowded adult leaves followed by the rapid formation of bracts and their axillary fascicles of small flowers (FIG. 3). Since there is no clear

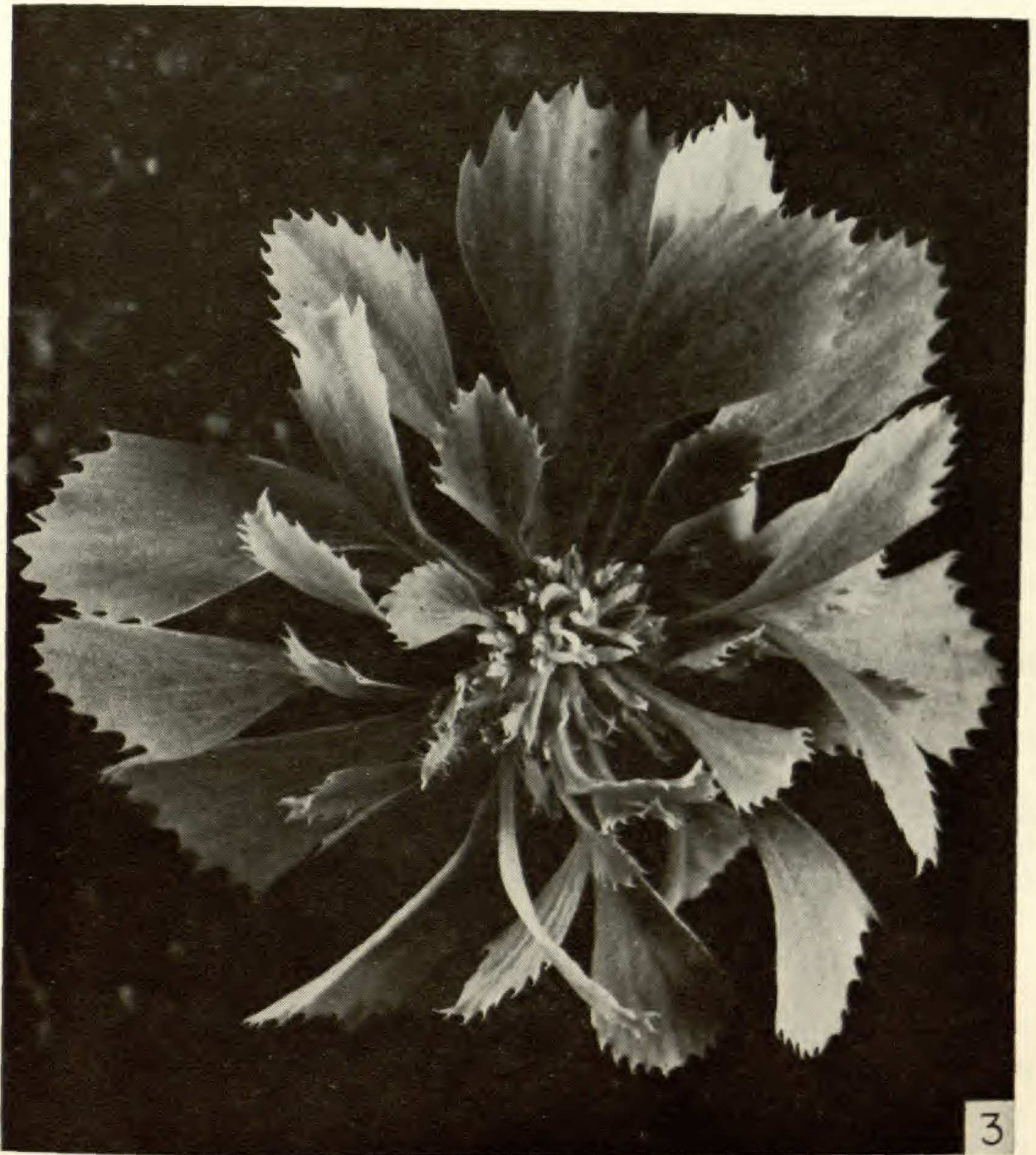


FIG. 3. A maturing cultivated specimen of *Circaeaster* showing the rosette of dichotomously veined leaves, the central fascicles of flowers and, at center left, a maturing fruit with characteristic uncinata hairs, $\times 3$.

demarcation either in form or venation between foliage leaves and well developed bracts, the latter were included in the total number of leaves in each of the 80 plants which were dissected and analysed in the present study (TABLE 1). Using this admittedly imprecise method of tabulation, it is nevertheless apparent that the number of leaves varies widely from plant to plant, ranging from 11 in very small precociously flowering individuals to as high as 180 in a few very robust plants. The "average leaf number" for *all* plants studied is approximately 60.

In an earlier paper (Foster 1963, p. 304) the question was raised whether the compact rosette of leaves and tiny flowers of mature plants is borne in an upright or prostrate position in nature. Cultivated plants, growing under the best horticultural conditions which could be provided,

throw some light on this question. During the maturing stages of these plants, many of them became "top heavy" and there was a marked tendency for the slender hypocotyl to be bent towards the ground. In fact it was necessary, in most cases, to use a miniature "Carnation-type" plant-supporter to hold each plant in a more or less erect position. In maturing plants in nature it seems possible that the rosette also may ultimately become prostrate but this conjecture needs to be tested by extensive field observations.

The full cycle of development in *Circaeaster* is relatively short and follows the general pattern of many dicotyledonous herbs. As accurately as could be determined, the life span of cultivated plants is about five months from seedling to complete maturity. This cycle is somewhat longer than that of the plants growing in their native habitat in Gangharea, North Garhwal, India, according to notes kindly given to me in a recent letter by Dr. M. A. Rau. He writes: "Regarding the growth cycle in nature, I do not have precise information about the time of appearance of seedlings. At these heights snow remains till the first week of June and it is, therefore, likely that germination takes place sometime during June. They are in full bloom by the middle of August and by the end of September the plants will have fruited. The plants are spent out by October and when I collected the ripe fruits on October 22 (1963), the fruits were all on the ground and the plants had collapsed. There may be some little variation in the dates given above from year to year depending on the environmental factors but in general you may take the above as the schedule in nature."

VEIN APPROXIMATIONS AND ANASTOMOSES

Résumé of Previous Studies. Before presenting the results of the present investigation, it seems highly desirable to review briefly (1) the classification i.e. "typology" of the anastomoses proposed in my recent paper (Foster 1966) and (2) to re-emphasize the morphological significance of vein approximations i.e. transitions between open dichotomous venation and true anastomoses. The latter represent the union between two xylem strands while in a typical vein approximation the tracheary elements of the adjacent branches of a pair of very closely spaced veins are separated by parenchyma (see Foster 1966, *Figs. 26, 27* for histological details).

The interrelationship between open dichotomous venation, vein approximations and Types I to III anastomoses are represented in FIG. 4. It should be emphasized that the very symmetrical vein approximation shown in this figure is not hypothetical but is based upon actual patterns observed in a number of leaves (Foster 1966, *Figs. 3, 4, 6, 8*). The distally "open" areole created by this kind of vein approximation is strikingly similar in form to the "closed" areoles formed by both Type I and Type II anastomoses. These two kinds of vein unions differ from each other in that xylem fusion in Type I is "transient," i.e. the extent of contact is relatively short while in Type II, the two veins completely merge to form a single, unbranched excurrent vein. Both of these forms of anastomoses are funda-

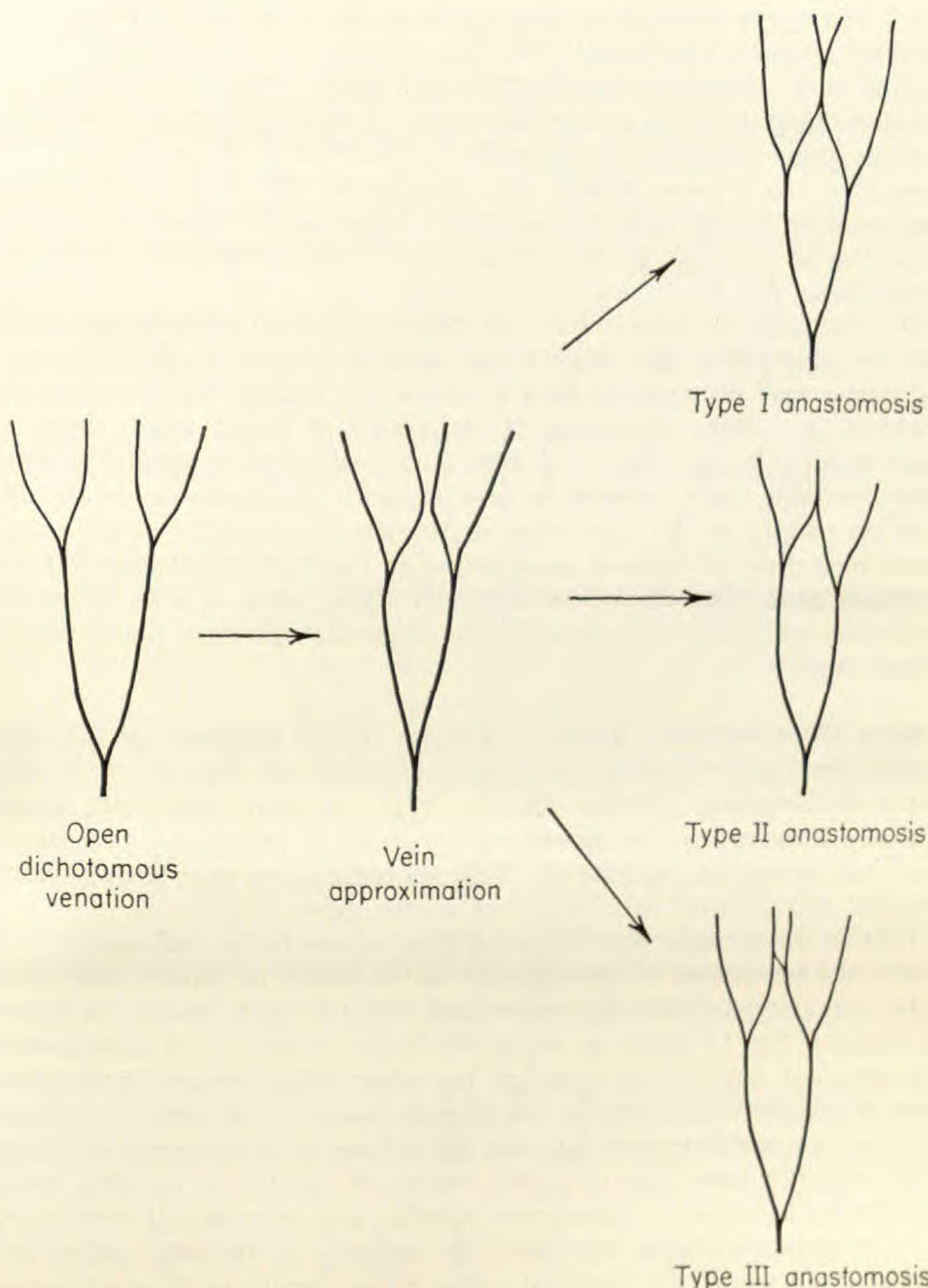


FIG. 4. Diagrams representing the morphological relationships between open dichotomous venation, symmetrical vein approximation and Types I to III anastomoses. Further explanation in text.

mentally similar however in that the union occurs between the adjacent branches of *two vein-dichotomies* (Foster 1966, *Figs. 1, 2*).

Type III anastomoses, as shown in FIG. 4, are less easily interpreted because the approximated branches of two vein-dichotomies remain discrete and are only interconnected by a very short obliquely oriented "commissural

vein." The xylem of the latter may consist of one or at most of only a few tracheary elements (see Foster 1966, *Figs. 28, 33a, b*). Whether the "commissural vein" should be regarded (1) as a much "reduced" branch of a vein-dichotomy or (2) as a "new formation" is problematical, although my previous study indicates a reasonable probability in favor of the first alternative. As I have pointed out, comparable difficulties arise in the interpretation of the short "commissural veins" in the leaves of certain ferns (Goebel 1922, pp. 19, 20) and in the petals of *Ranunculus* (Arnott & Tucker 1963, *Fig. 16*, type C").

Although multiple anastomoses (i.e. two or more vein unions in one leaf) were not observed in any phase of my investigations on *Circaeaster*, several leaves were encountered each of which had formed two vein-approximations. A striking illustration is represented in FIG. 5 which shows a small bract (13 mm. long \times 3 mm. wide) with two symmetrical vein approximations, each forming a very elongate distally open areole. A venation pattern of this type suggests the strong possibility of the occasional formation of multiple anastomoses in *Circaeaster* but thus far no examples have been discovered either in leaves from a wide range of herbarium specimens or in those of the numerous cultivated plants which I have studied.

New Observations. TABLE 1 provides further evidence for the conclusion previously reached that anastomoses are very uncommon in the leaves of *Circaeaster* (Foster 1966, p. 592). In more than 5000 leaves critically examined in the present survey, only 54 or about 1 percent of them had formed an anastomosis. Vein approximations were slightly more frequent and occurred in 2 percent of all the leaves studied.

Despite the sporadic distribution of anastomoses in the leaf sample *as a whole*, the percentage of anastomoses in the leaves of certain *individual plants* was comparatively high and ranged from 1.8 to 6.6 percent. As shown in TABLE 2, the 12 plants in which this higher frequency of anastomoses was observed, were distinct from all the other plants because of the presence of solitary vein-unions in two or more leaves of the same individual. It seems reasonable to postulate that the number of anastomoses per plant may be under some type of genetic "control" but this is an idea which requires confirmation by appropriate breeding and experimental techniques.

From a morphological viewpoint, the majority of the vein unions analysed could readily be classified under either Type I or II anastomoses (FIG. 4). But 22 percent of the anastomoses found in the present survey are sufficiently distinctive to justify their segregation into new categories which for convenience are designated as Types IV and V. (FIG. 6).

In both of the new types of anastomoses, the areole is formed by the union between an *unbranched arcuate vein* and one of the branches of its sister vein lying above it (FIG. 14). This pattern is clearly different from that represented by Types I to III anastomoses in which union occurs between two of the branches of a *pair* of adjacent vein dichotomies (cf. FIGS. 4 and 6). As shown diagrammatically in FIG. 6, Types IV and V

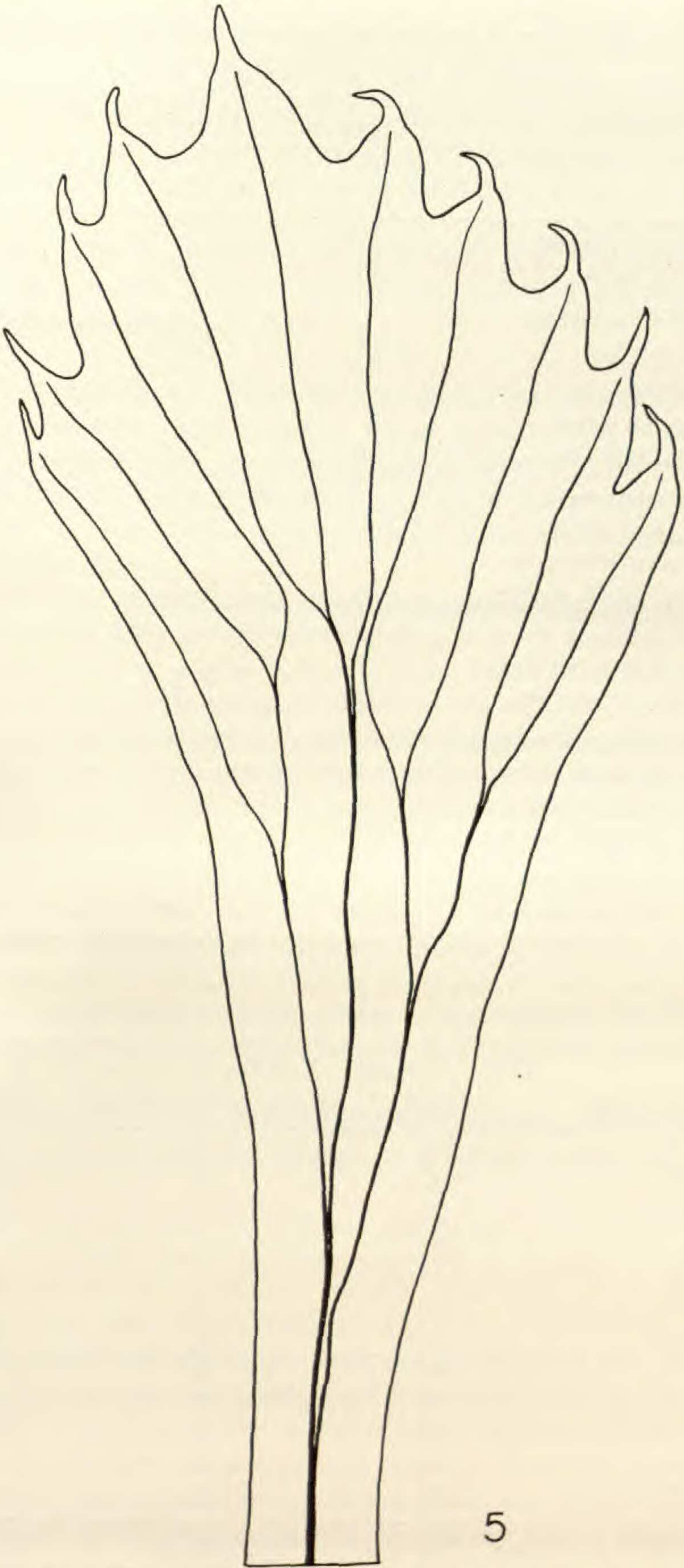


FIG. 5. Floral bract showing the rare occurrence in *Circaeaster* of two vein approximations, each forming a greatly elongated areole "open" at its distal end, $\times 24$.

TABLE 1. Summary of anastomoses and vein approximations in leaves of cultivated plants of *Circaeaster agrestis*

| | PLANTS GROWN IN 1965 | PLANTS GROWN IN 1966 | TOTALS |
|--|----------------------------|----------------------------|--------|
| TOTAL NUMBER OF PLANTS | 40 | 40 | 80 |
| TOTAL NUMBER OF LEAVES | 2248 | 2772 | 5020 |
| NUMBER OF LEAVES WITH ANASTOMOSES | 29 | 25 | 54 |
| NUMBER OF PLANTS WITH ANASTOMOSES IN 2 OF MORE LEAVES | 8 | 4 | 12 |
| NUMBER OF LEAVES WITH VEIN APPROXIMATIONS | 45 | 75 | 120 |
| NUMBER OF PLANTS WITH VEIN APPROXIMATIONS IN 2 OR MORE LEAVES | 11 | 18 | 29 |
| % OF LEAVES WITH ANASTOMOSES | 1.2 | 0.9 | |

TABLE 2. Percent of anastomoses in plants with vein unions in two or more leaves

| PLANT NUMBER | TOTAL NUMBER LEAVES | NUMBER OF LEAVES WITH ANASTOMOSES | % OF LEAVES WITH ANASTOMOSES |
|--------------|------------------------|--------------------------------------|---------------------------------|
| 5a | 30 | 2 | 6.6 |
| 15a | 109 | 2 | 1.8 |
| 16a | 93 | 2 | 2.1 |
| 27a | 109 | 3 | 2.7 |
| 29a | 145 | 3 | 2.0 |
| 33a | 80 | 2 | 2.5 |
| 34a | 45 | 2 | 4.4 |
| 35a | 45 | 2 | 4.4 |
| 4b | 95 | 2 | 2.1 |
| 19b | 80 | 2 | 2.5 |
| 21b | 84 | 4 | 4.7 |
| 26b | 60 | 4 | 6.6 |
| TOTALS | 975 | 30 | |

anastomoses are morphologically connected, by corresponding vein approximations, with an asymmetrical form of open dichotomy which commonly occurs in the leaves of *Circaeaster*. This pattern is termed "asymmetrical" because one of the derivatives of a vein-dichotomy remains unbranched throughout its course while its sister derivative bifurcates one or more times before reaching the distal margin of the lamina (Figs. 9, 11, 18, 21, 23).

With the preceding analysis as a general basis, it is now appropriate to describe in detail the new forms of anastomoses and their interrelationships with vein approximations.

Type IV Anastomoses. The distinguishing character of this type of anastomosis is the very short extent of xylem-contact between the arcuate vein and the branch of a contiguous vein-dichotomy (Fig. 6). After separation of the two strands, the upper portion of the arcuate vein either terminates in a marginal tooth or ends blindly in the lateral margin of the lamina (Figs. 11, 13).

The resemblances between vein approximations and Type IV anastomoses are indeed striking and support the idea that the two patterns differ from one another only in degree (compare Figs. 7, 10, 11). In some cases, a relatively wide strip of parenchyma separates the region of approximation between the arcuate vein and its contiguous strand (Fig. 8). But very commonly, the interval is so narrow that it is impossible to draw a distinction between an anastomosis and a vein approximation until a leaf has been thoroughly cleared in NaOH and chloral hydrate. Fig. 7 is a good example of this because it shows the extremely close approximation between the two veins at the upper left margin of the leaf. Additional illustrations of closely approximated veins are evident in Figs. 9, 10, and 12.

Type V Anastomoses. In this type of vein union, the tip of an arcuate unbranched vein converges toward and becomes confluent with the branch of a vein-dichotomy situated above it. Two "variations" of this kind of anastomosis have been discovered and, as is shown in Fig. 6, each of them is morphologically related to a corresponding type of vein approximation.

In the simpler of the two "variations," the arcuate vein joins the outer branch of a *first order* vein-dichotomy, creating a conspicuous and relatively symmetrical areole (Figs. 14, 16-19). The exact point of anatomical union between the xylem strands fluctuates. Commonly the two xylem strands merge well above the level of the adjacent vein dichotomy (Figs. 14, 16-18) but the union may take place very near the point of bifurcation of the vein (Fig. 19). An interesting example of the arrested development of a Type V anastomosis is shown in Fig. 15. Examination of this leaf under high magnification reveals that the terminal tracheary elements of the marginal arcuate vein at the left are not in direct contact with the xylem of the neighboring vein, and hence that the areole is of the "open" type.

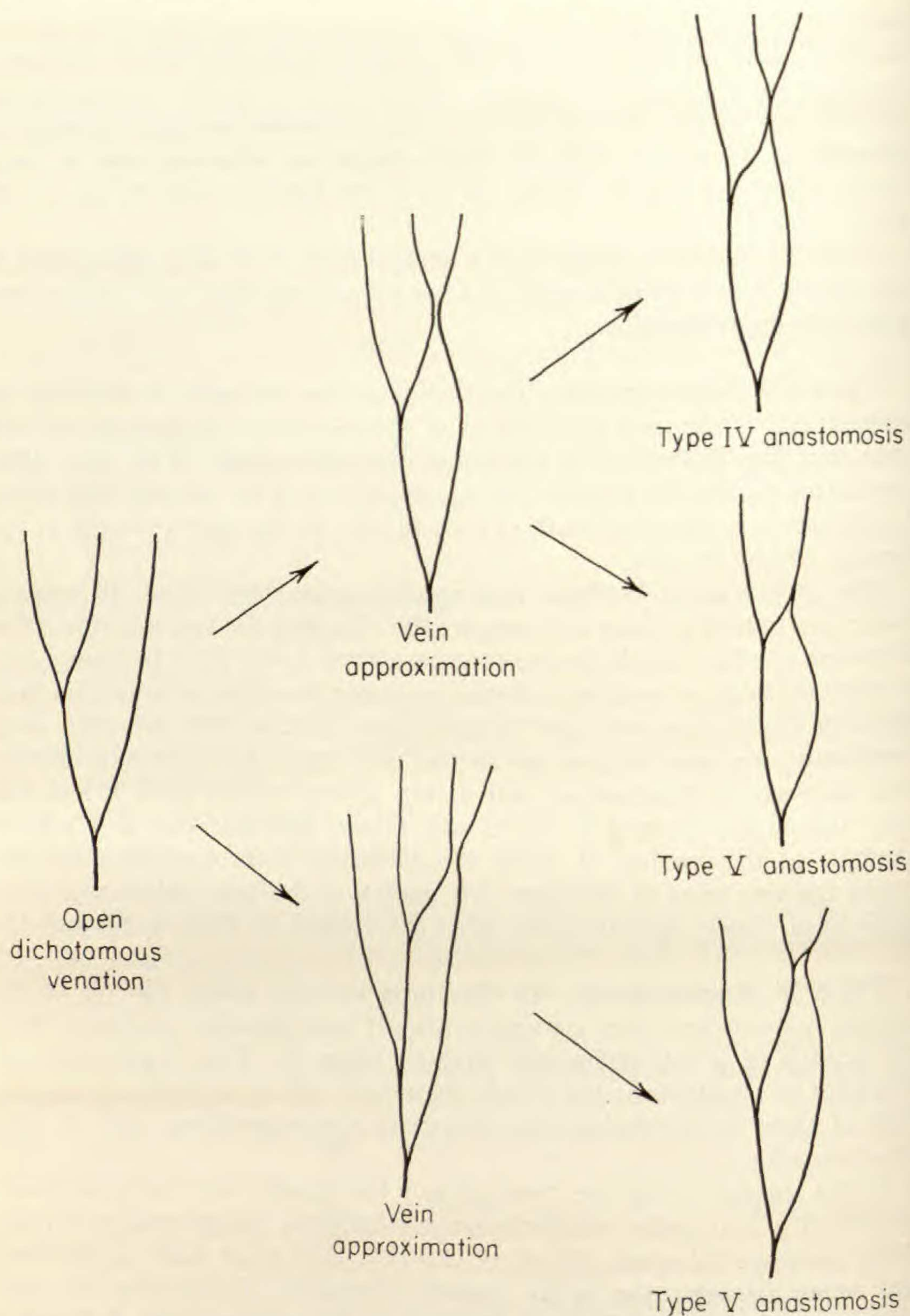


FIG. 6. Diagrams representing the morphological relationships between open dichotomous venation, vein approximations, and Types IV and V anastomoses. Further explanation in text.

In the other Type V "variation," an areole is created by the union of the arcuate vein with the outer branch of a *second order* vein-dichotomy lying above it (FIGS. 6, 21-23). Vein approximations which morpholog-

ically connect such anastomoses with open venation are not common but the leaf shown in FIG. 20 apparently developed such a transitional form.

When examples of Types IV and V anastomoses were first encountered in this survey it seemed possible that they might be restricted to that part of the vein system adjacent to the lateral margins of the lamina. (FIGS. 13, 16, 21, 22). Further study however clearly indicated that both of the new types of anastomoses may also occur in a more central position in the venation (FIGS. 11, 18, 19, 23).

DISCUSSION

The various forms of vein approximations which occur in the leaves of *Circaeaster* are regarded as morphological "transitions" which connect the different types of anastomoses with open dichotomous venation (FIGS. 4-7). This conclusion seems fully justified by the present comprehensive survey and it is important in this connection to note that "near fusions" of veins were also observed by Arnott (1959, p. 408) in the foliage leaf of *Ginkgo* and by Arnott and Tucker (1963, p. 822) in the petals of *Ranunculus repens* var. *pleniflorus*. In both of these examples, anastomoses are considerably more frequent than in *Circaeaster* but the fundamental pattern of venation is dichotomous. It is of further comparative interest that anastomoses and vein approximations remarkably similar to those in *Circaeaster*, also occur in the dichotomous venation of certain living ferns. In a brief unpublished study on the venation of *Anemia herzogii* Rosenstock, I observed that the most common types of anastomoses correspond to Types I and II (see FIG. 4). In proportion to the relatively high number of dichotomously branched veins in each pinna however, anastomoses and their coordinated types of vein approximations in this fern seem just as sporadic and "unpredictable" in position as in the leaves of *Circaeaster*.¹

These brief comparisons between *Circaeaster* and other living taxa with dichotomously veined foliar appendages clearly support my concept that a parallel evolution of similar types of anastomoses has very probably occurred in morphologically divergent and taxonomically unrelated plants (see also Foster 1961, p. 974 and 1966, pp. 596, 599). But even with this idea in mind, the question nevertheless arises as to the original or most ancient type or types of vein anastomoses in vascular plants as a whole.

Although there appear to be very few published descriptions of the details of venation patterns in extinct groups of the Pteropsida, Types I and II anastomoses, as defined in the present paper, seem to represent extremely ancient trends in the evolution of areolate venation. Both of these types

¹ According to Mickel's (1962) study on *Anemia*, the pinnae of species classified in the subgenus *Coptophyllum* are open dichotomously veined and devoid of anastomoses while in the subgenus *Anemia*, weakly anastomosed (e.g. *A. herzogii*) or conspicuously areolate venation (e.g. *A. phyllitidis*) is typical. It is of considerable interest that in *A. × ulbrichtii*, a hybrid between *A.* (subg. *Coptophyllum*) *raddiana* and *A.* (subg. *Anemia*) *phyllitidis*, the venation is "intermediate" in character, i.e., rather weakly anastomosed. An intensive study of venation patterns throughout the genus *Anemia* is obviously highly desirable.

of vein unions were observed in *Neuropteris* and other fern-like plants of the Paleozoic by Potonié (1912, pp. 111–117) and Type II anastomoses evidently created the lax areolate venation characteristic of various species of *Ctenis* (Florin 1933, pp. 53–80) and *Gangamopteris* (Zimmermann 1959, p. 284 and *Fig. 148b*). Very recently, my attention has been kindly directed, by Mr. William Glen of the Department of Paleontology at Berkeley, to the illustrations of typical Type II anastomoses in *Psygmo-phyllum flabellatum* (= *Ginkgophyton flabellatum*) given by Seward (1919, p. 83, *Fig. 666*). In this Paleozoic plant of uncertain affinities, Seward observed that “the veins spread from the base of the lamina and are repeatedly forked; they may be very numerous and in some forms occasionally anastomose, as in *P. flabellatum*” etc.

On the other hand, how should one interpret phylogenetically the apparently extremely simple type of anastomosis in which an areole is created by the union of the two branches of a single vein-dichotomy? Is this form of anastomosis, which is the most common type in *Ginkgo* (Arnott 1959, *Fig. 3*), “primitive” or “advanced” in vascular plants as a whole? As far as I am aware, this kind of anastomosis, designated as “Type A” by Arnott, has not been recorded in paleobotanical literature. In living plants aside from *Ginkgo*, however, “Type A” anastomoses occur in the dichotomous venation of certain cycads (e.g. *Stangeria*, *Dioon*, *Encephalartos*, and *Zamia*), in a few ferns which I have personally examined such as *Stenochlaena palustris* (Burm.) Bedd. and *Anemia herzogii* Rosenstock, and in the petals of *Ranunculus* where, however, they are very infrequent (Arnott & Tucker 1963, p. 827). A single example of a “Type A” anastomosis was found in my survey of *Circaeaster* but the leaf in which it occurred was so damaged in processing that it had to be discarded. In a few leaves, as illustrated by *FIG. 24*, a very rare type of vein approximation was noted which might be regarded as “transitional” between a “Type A” anastomosis and a normally bifurcated vein. It should be clear from this brief discussion, however, that the “phylogenetic status” of “Type A” anastomoses in the living ferns and seed plants must for the present remain an entirely open question.

There remains for final consideration the morphology and possible phylogenetic significance of Types IV and V anastomoses (*FIGS. 6, 14*). I know of no record of these forms of anastomoses in extinct tracheophytes but I have seen excellent examples of Type V unions in the marginal veins of certain pinnae in the leaves of *Anemia herzogii*. Among angiosperms, Type V anastomoses are abundantly formed during the ontogeny of the venation in the cotyledons of *Pulsatilla vulgaris*. In this case, the anastomoses are interpreted by Höster and Zimmermann (1961, pp. 85, 86, p. 93 and *Figs. 12–14*) as morphologically comparable with the “Goniopteridis” type of vein union previously recognized by Zimmermann (1959, p. 277, *Fig. 142*) as primitive in his phylogenetic series of reticulate venation patterns in “Pteridophylls.” Type V anastomoses are also common in the dichotomous venation of the petals of *Ranunculus*. Arnott and Tucker (1963, 1964) regard these anastomoses as a “variation” of their “Type C” vein union

(= Type II anastomosis in *Circaeaster*). On the basis of these few, scattered examples it is clearly impossible, however, to reach a phylogenetic conclusion, although I suspect that both Types IV and V anastomoses ultimately may prove to be relatively "primitive" in an evolutionary sense.

In conclusion, I wish to emphasize the need for more detailed attention by paleobotanists to the diversified trends of specialization of areolate venation in extinct members of the Tracheophyta. It should be more widely recognized, in my opinion, that the presence or absence or *degree* of development of anastomoses in any given system of dichotomous venation has phylogenetic significance in addition to its diagnostic importance for purposes of identification and classification. The same viewpoint is justified, I believe, with reference to the occurrence of dichotomous venation and sporadic anastomoses in the leaves of certain living seed plants. An excellent illustration is provided by Arnott's (1959) discovery of various types of anastomoses in the dichotomous venation of such a "living fossil" as *Ginkgo biloba*. Napp-Zinn (1966, p. 166) in his review of leaf anatomy in gymnosperms points out that anastomoses also occur in the dichotomous venation of two living genera of cycads (e.g. *Stangeria* and *Macrozamia*). In a study of leaf venation in *Zamia* now in progress, I have found striking examples of anastomoses entirely comparable, *in a morphological sense*, to the Types I and II vein unions which occur in the leaves of both *Kingdonia* (Foster 1959, Foster & Arnott 1960) and *Circaeaster* (Foster 1966). Whether the venation patterns in these two remarkable dicotyledons represent (1) the "retention" of a condition which appeared during the early evolution of angiosperms or (2) are the result of "reversion" from a more complex vasculature, are questions which cannot be convincingly answered until future paleobotanical discoveries have clarified the origin and major trends of phylogeny of the angiosperms as a whole.

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EXPLANATION OF PLATES

PLATE I

FIG. 7. Cleared leaf showing, at left, the approximation between an unbranched vein and a branch derived from an adjacent vein-dichotomy. This type of vein approximation is represented diagrammatically in FIG. 6, $\times 14$.

PLATE II

FIGS. 8–13. Venation patterns showing intergradations between vein approximations and Type IV anastomoses. FIG. 8. "Open" marginal areole at upper left formed by convergence and abrupt divergence of two adjacent veins, $\times 5$. FIG. 9. Vein approximation similar to one in FIG. 8 but the two veins nearly confluent, $\times 3.8$. FIG. 10. Very close approximation between two veins forming an elongated "open" submarginal areole, $\times 7$. FIG. 11. Leaf with a Type IV anastomosis which closely resembles the pattern of the vein approximation shown in FIG. 10, $\times 5.3$. FIG. 12. Vein approximation forming an exceptionally small "open" submarginal areole, $\times 4.2$. FIG. 13. Leaf with a Type IV anastomosis (lower right margin) formed by the transient union between an unbranched blindly terminating vein and the adjacent branch of a vein-dichotomy, $\times 4.5$. US, unconnected vascular strand.

PLATE III

FIG. 14. Small floral bract showing, near the middle of the lamina, a striking example of a Type V anastomosis, $\times 32$.

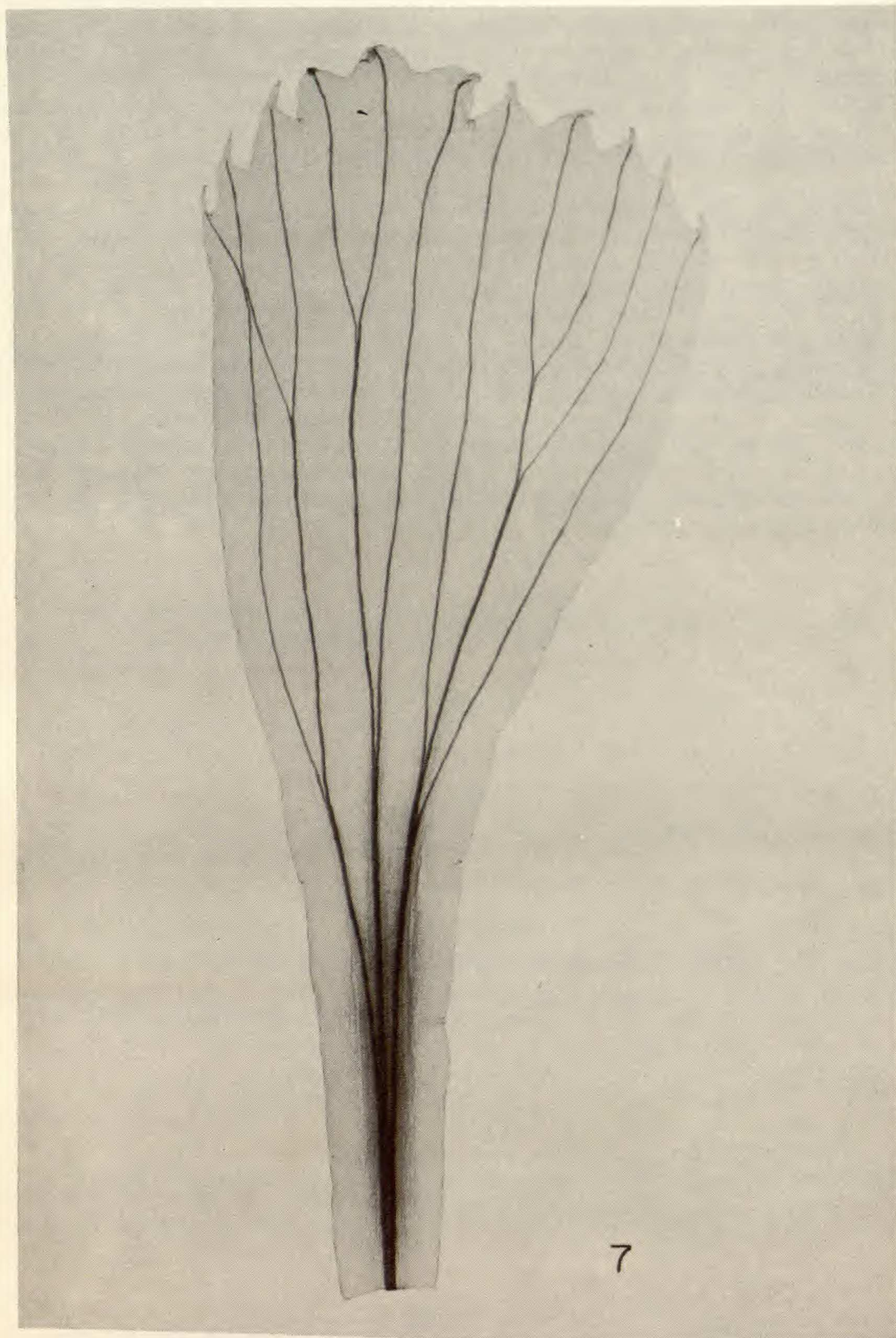
PLATE IV

FIGS. 15–19. FIG. 15. An unusual type of an "arrested" anastomosis in which the tip of the unbranched arcuate xylem-strand at the left margin ends a few

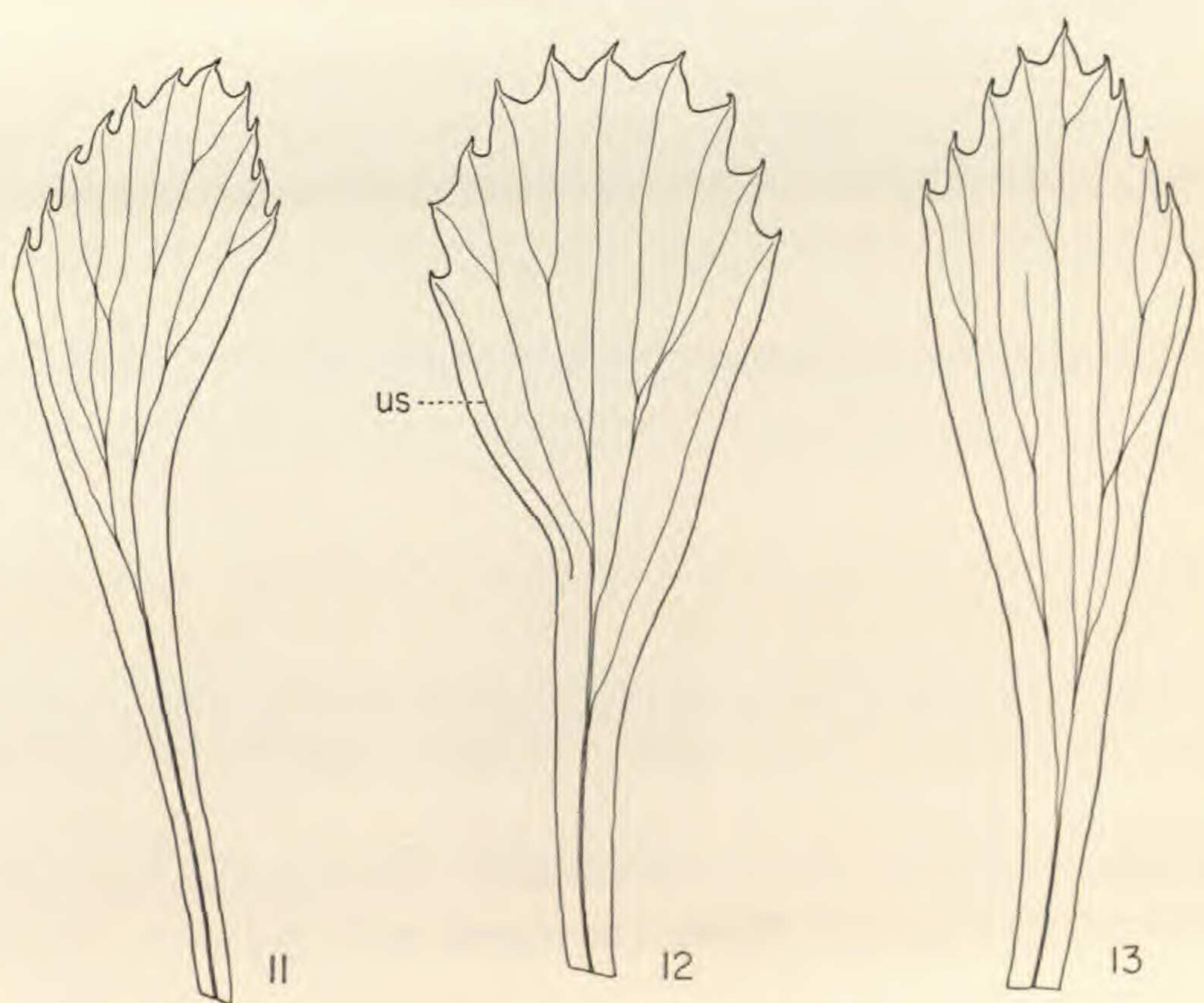
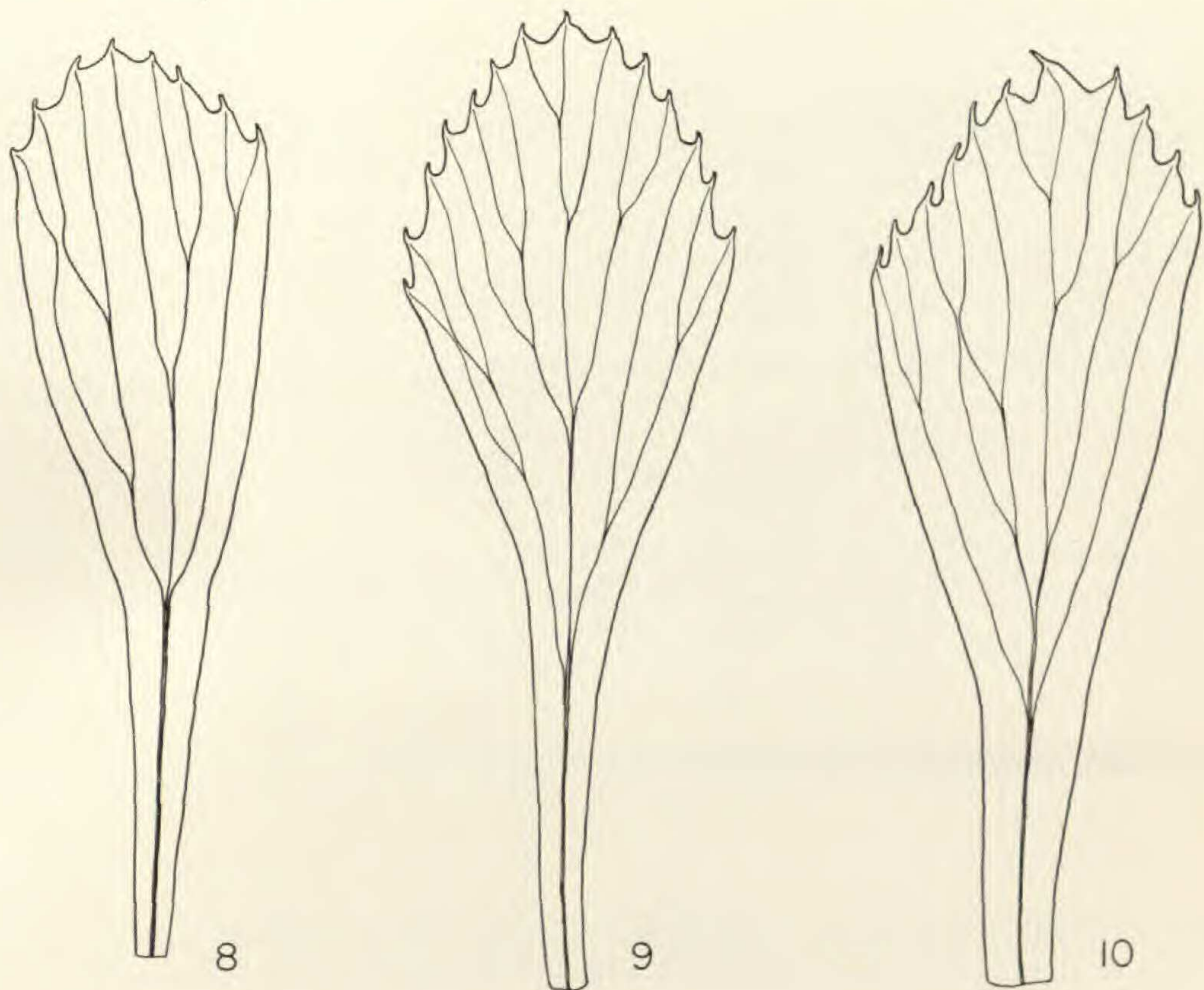
cells below the outer branch of the vein-dichotomy lying above it, $\times 7$. FIGS. 16–19. Various examples of Type V anastomoses. FIG. 16. Primary leaf with anastomosis at right margin of lamina, $\times 5.5$. FIG. 17. Typical adult type of foliage leaf showing a conspicuous submarginal areole, $\times 3.8$. FIG. 18. Similar example of Type V anastomosis forming a smaller submarginal areole, $\times 7$. FIG. 19. An example of vein union below the point of separation of the branches of a vein-dichotomy. Note blind vein-ending *between* two marginal teeth at lower left side of lamina, $\times 5.5$. *US*, unconnected vascular strand.

PLATE V

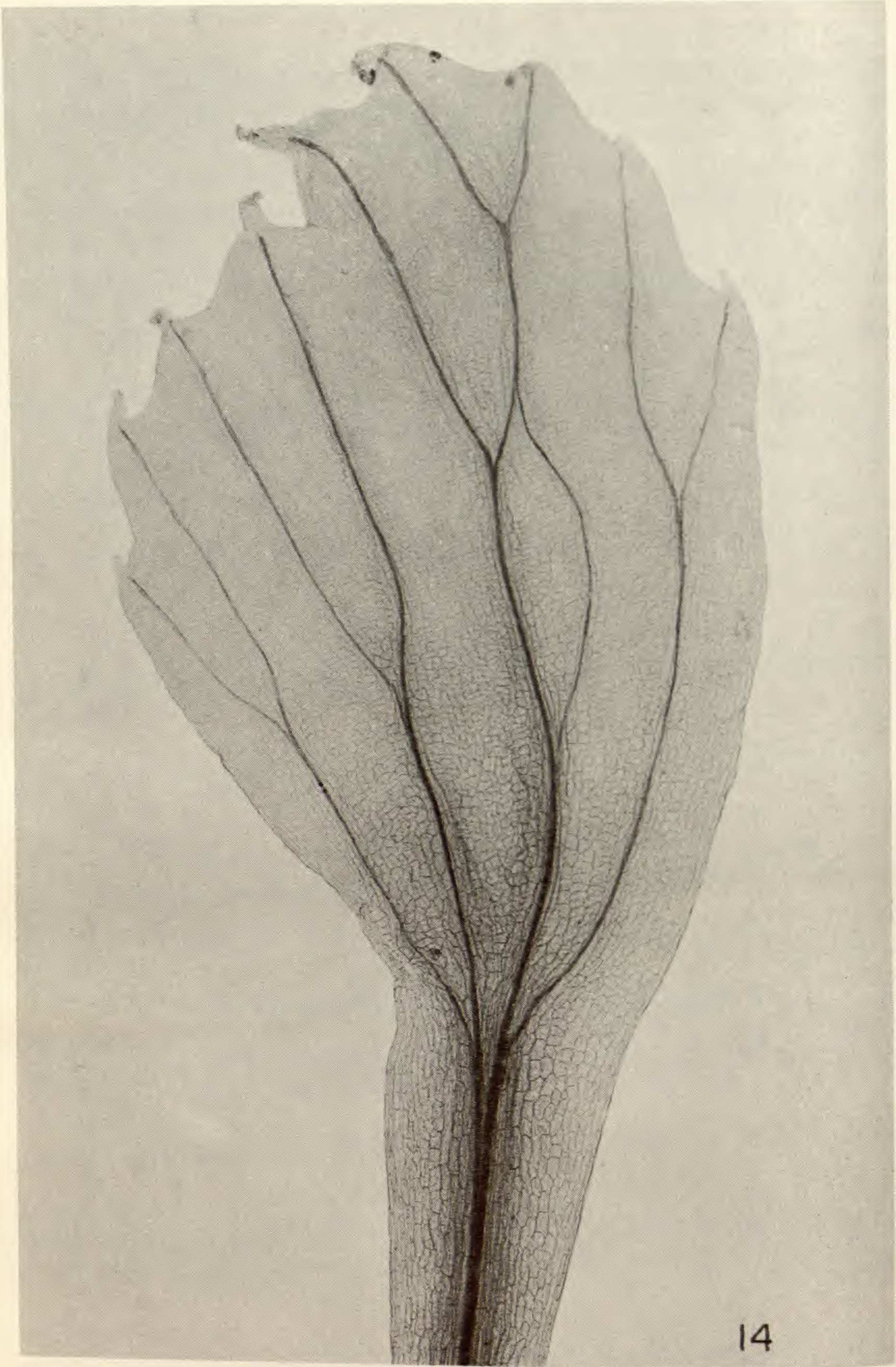
FIGS. 20–24. FIG. 20. Leaf illustrating approximation between marginal vein (at right) and adjacent branch of second order vein-dichotomy. This type of vein approximation is shown diagrammatically in FIG. 6, $\times 6$. FIGS. 21–23. Various examples of Type V anastomoses morphologically related to the kind of vein approximation shown in FIG. 20. FIG. 21. Primary leaf in which a vein anastomosis produced a large marginal areole, $\times 4.5$. FIG. 22. Floral bract with a smaller anastomosis similar in position and type to that shown in FIG. 21, $\times 7$. FIG. 23. Conspicuous Type V anastomosis in upper central region of lamina, $\times 5.5$. FIG. 24. Leaf with very uncommon type of vein approximation (at left margin) in which the branches of a single vein-dichotomy converge and then separate without xylem-fusion, $\times 4.8$. *rt*, rudimentary marginal tooth; *US*, unconnected vascular strand.



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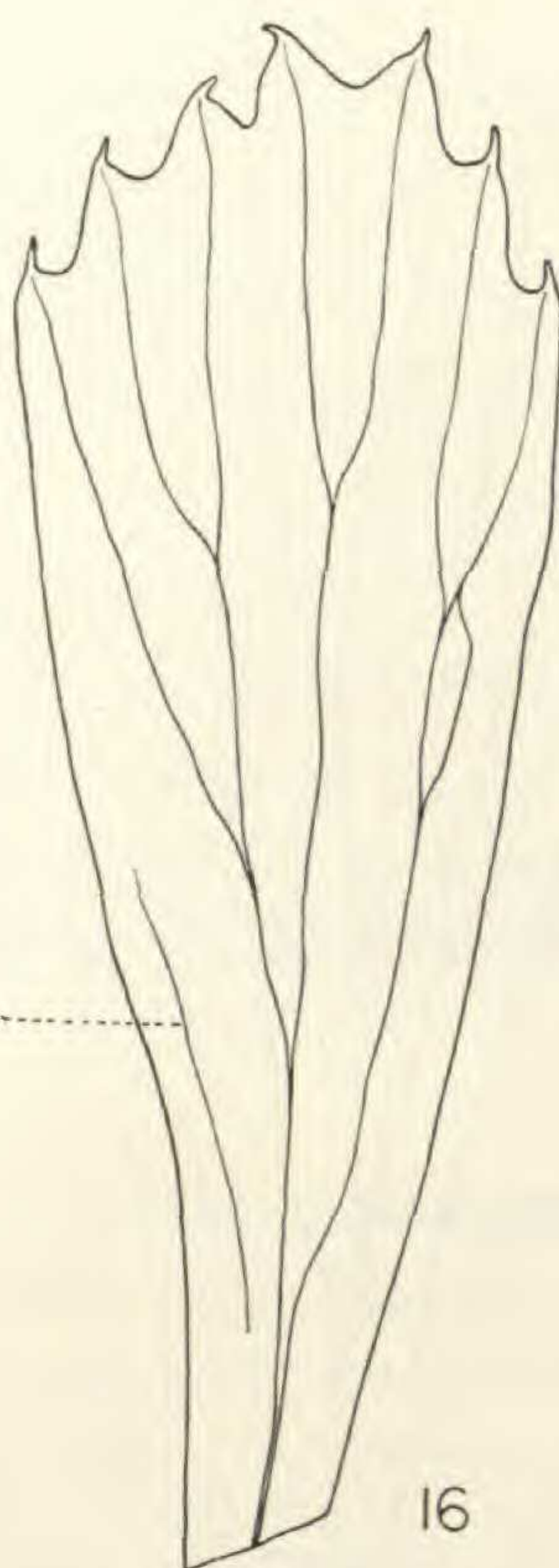


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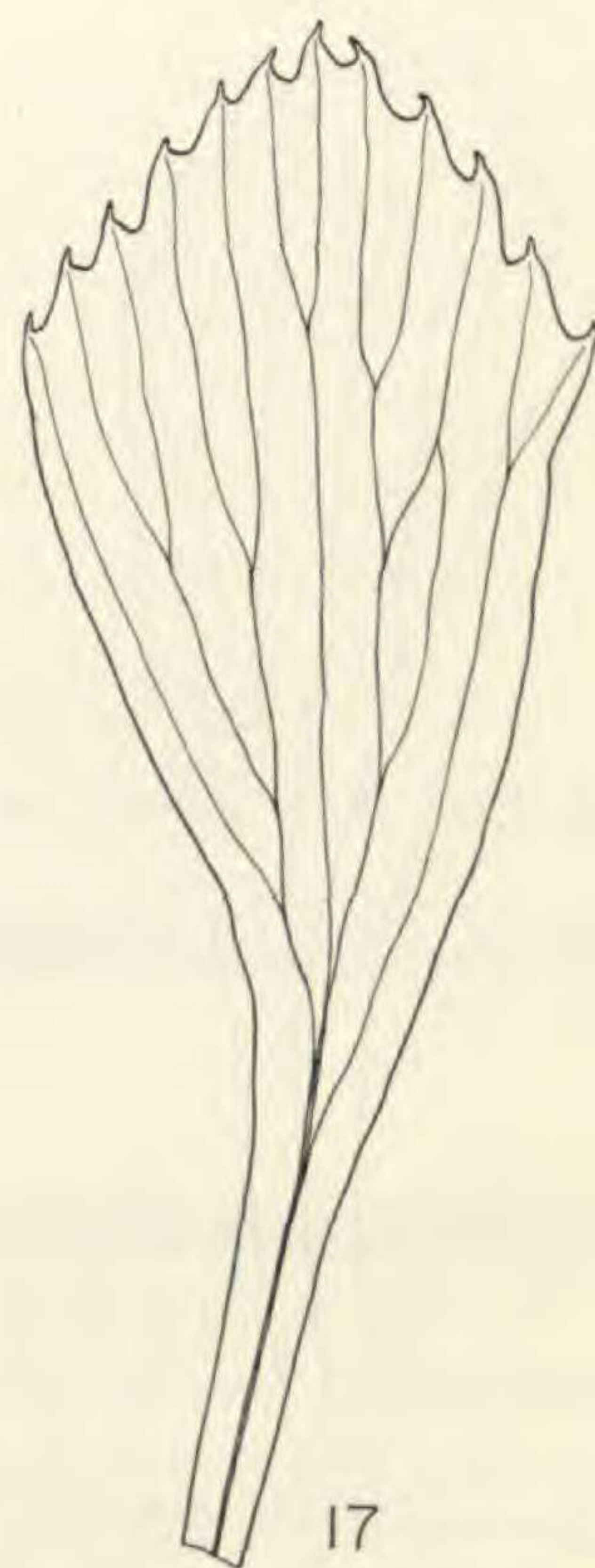


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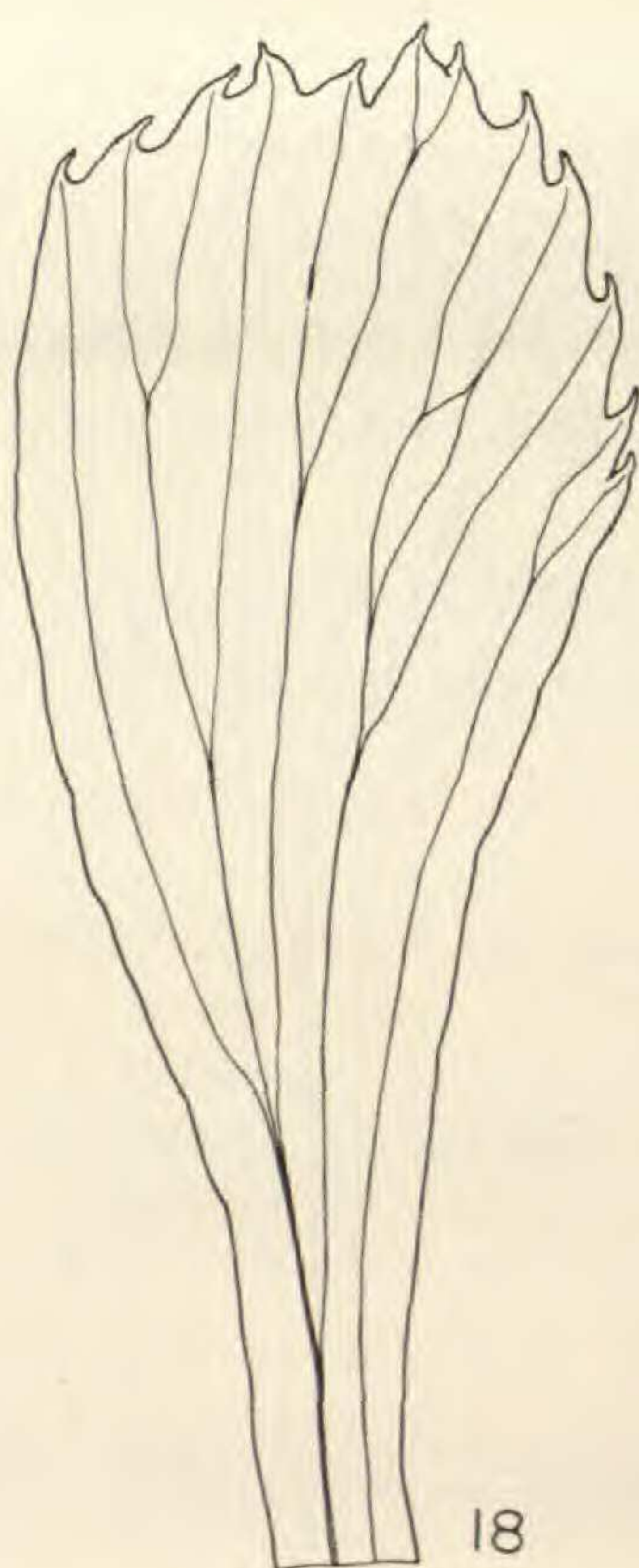
US



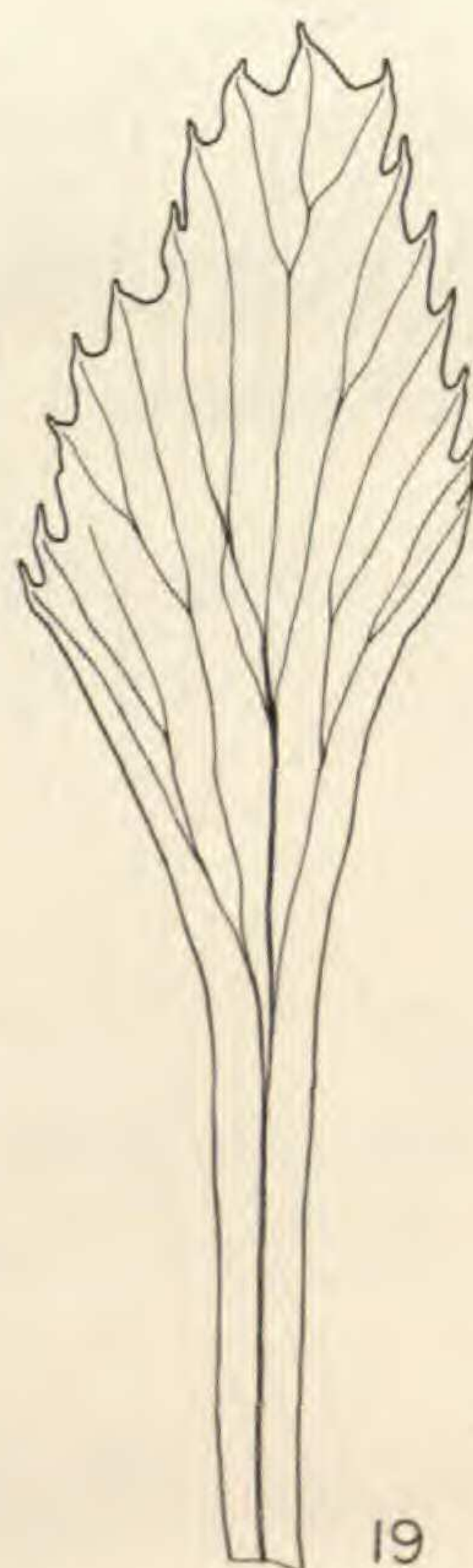
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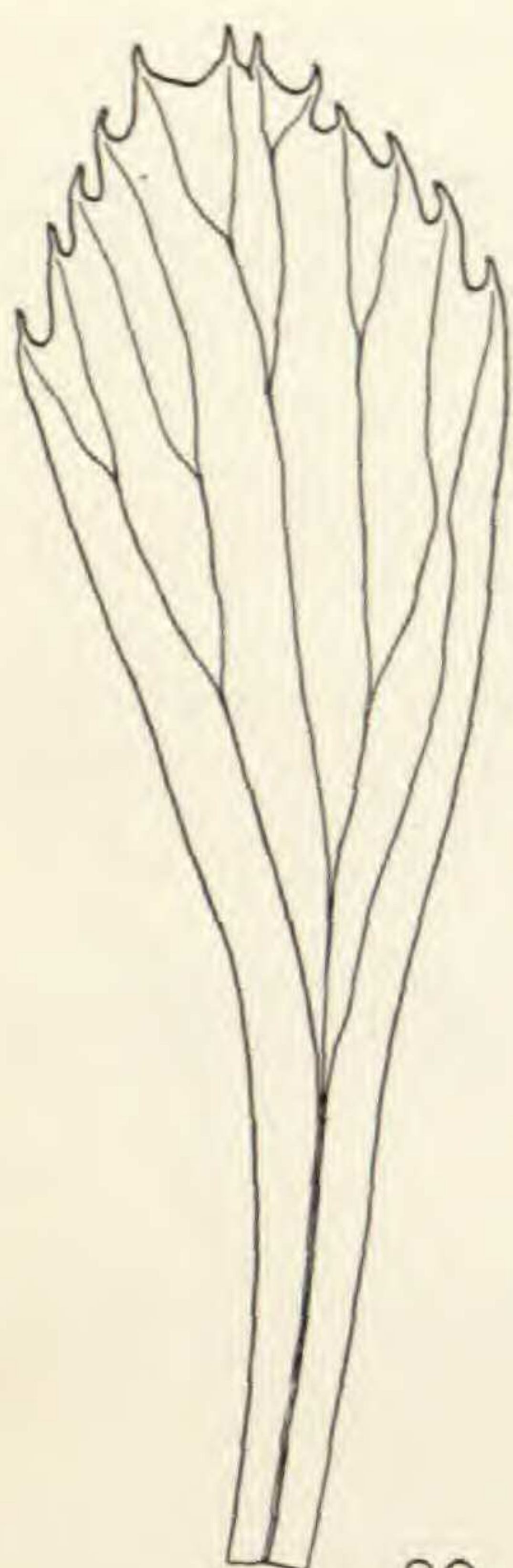


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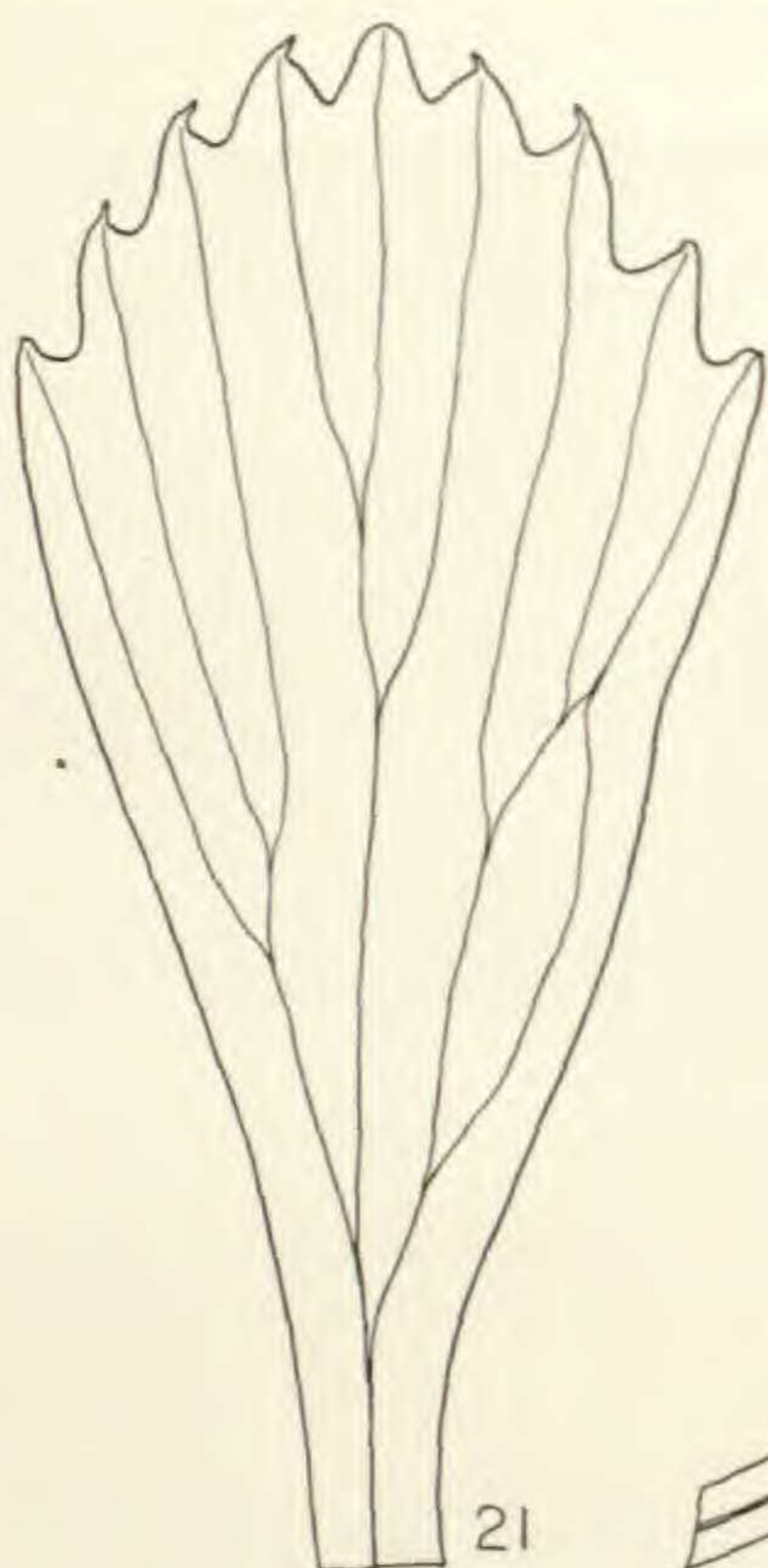


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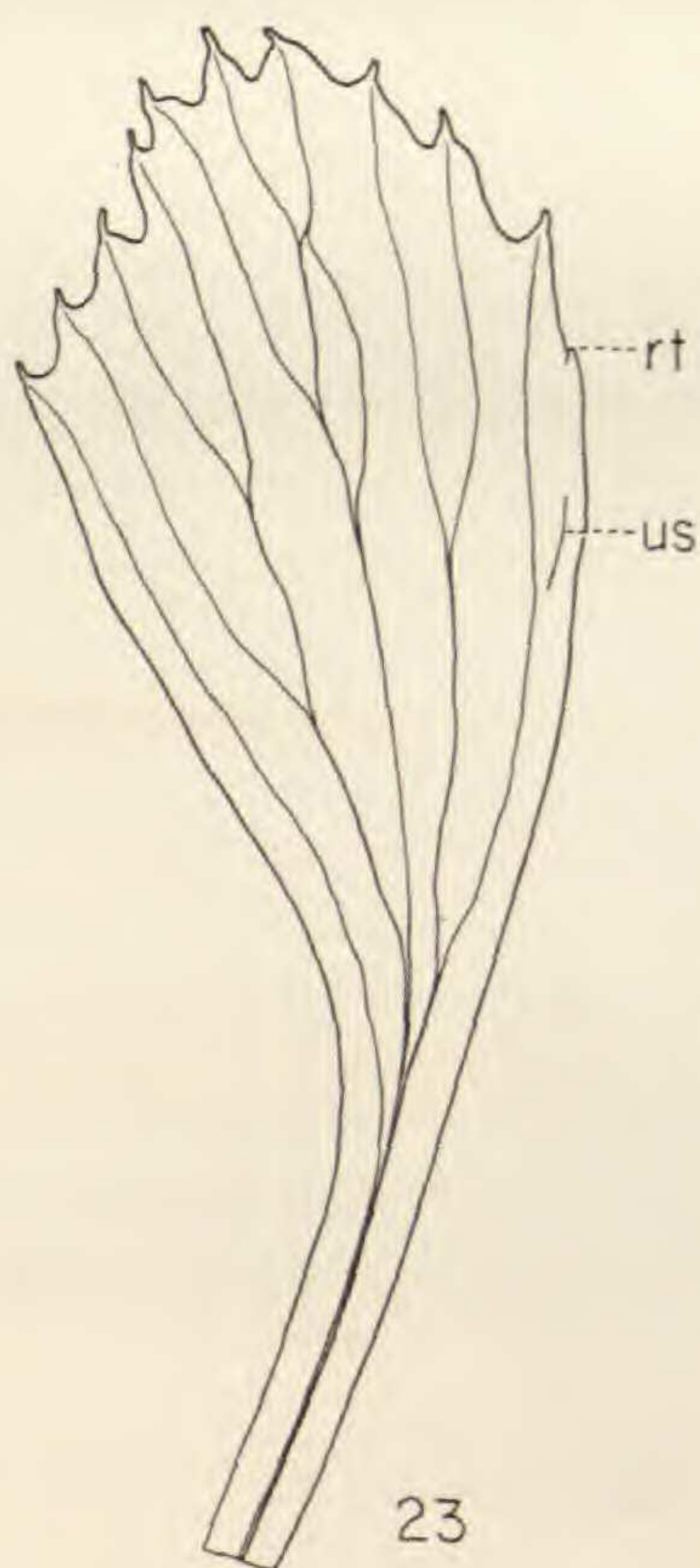
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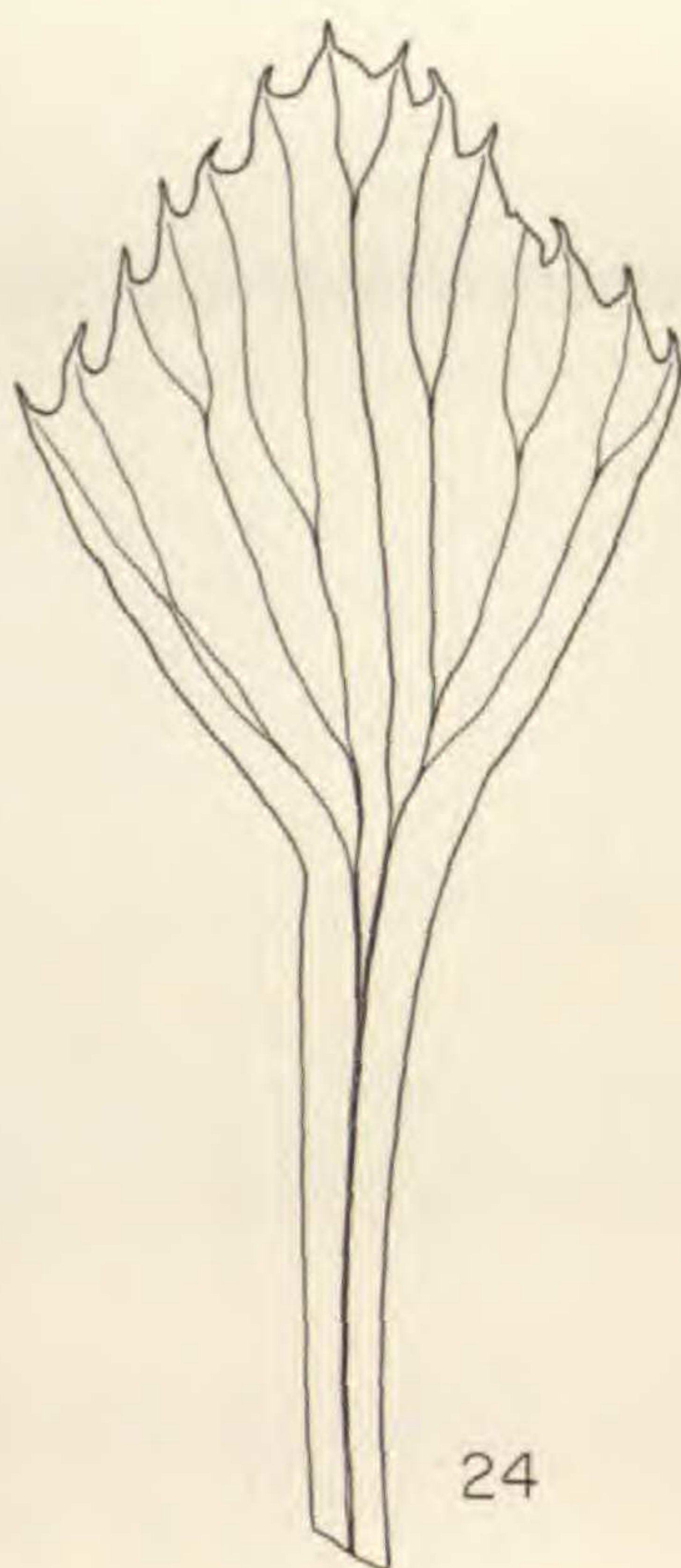
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